A08860

Reprinted from *Wildfowl Trust 18th Annual Report* (1967), pp. 106-121

Breeding behaviour of captive Shovelers

F. McKINNEY, Minnesota Museum of Natural History, Minneapolis, Minnesota 55455, U.S.A.

Summary

The breeding behaviour of full-winged Shovelers was studied in flight pens measuring 0.15 and 0.19 acre during five seasons. Thirty-one pairs were observed, mostly in groups of four pairs per pen. Only three pairs failed to breed, but hatching success was poor and few ducklings were raised to maturity.

After introduction to the pen, usually in early May, pairs were sociable for a few days but soon established well defined territories. Females began inspecting nesting cover, during the first few hours after dawn, as early as 27 days before laying. Time spent in cover each day increased on the days before laying and continued to increase during laying.

Copulations were frequent in the pre-laying period but decreased during laying and were rare during incubation. Pairs often copulated twice each day before laying began, but no clear preference was shown for certain times of day. Most mountings resulted in apparently successful copulation (120 records); some males slipped off before intromission (10 records); in 15 cases, pairs were interrupted by the approach of other birds. Apparently successful rape of strange females was seen only four times.

Pairs made flights around the pen and some females gave Persistent Quacking during May, but both activities stopped as soon as egg-laying began. Visits to the nest for laying were usually in the morning. Eggs were laid at a rate of one per day, but sometimes a day was skipped. Incubating females left the nest most often in late morning or in the afternoon, but there was much variation.

The number of eggs decreased in many nests during incubation. There was no evidence of predation. Three observations of females flying from the nest carrying an egg in the bill suggested that this behaviour accounts for the disappearing eggs. The eggs seemed to be pierced and carried in the tip of the bill, but whether the eggs removed were addled, and how they became broken is unknown. There is no evidence that Shovelers remove the shells from which ducklings have emerged.

Chasing activities peaked in frequency just after dawn and were followed by a period of sleeping during the middle and late morning. On some days there appeared to be a second peak in the number of birds sleeping in the afternoon. Chasing and sleeping were infrequent in the last hour or so before sunset, probably because feeding activity increased at that time.

Seasonal and daily patterns of activity in the flight pens agreed with what is known of schedules in the wild, but the captive conditions had serious effects on breeding success. Brood behaviour was most strikingly influenced by the crowding and restriction of movement. Females with broods attacked strange ducklings and probably killed some. But the high duckling losses were likely caused mainly by shortage of preferred food in the pens.

A considerable amount of information on the breeding biology of a number of duck species has accumulated during the last 25 years through intensive field studies. For the commoner species, many papers describe nesting sites, clutch- and brood-sizes, and breeding success. Certain kinds of information on breeding behaviour, however, have proved extremely difficult to obtain in the field. In particular, there are many gaps in our knowledge of topics requiring prolonged observations on marked individuals of known age and breeding status. For example, there is little precise information on the chronology of activities in individual pairs during the breeding season, variations in behaviour dependent on time of day, and interactions between breeding pairs. While it is often possible to get the general picture from observations in the wild, it is usually very difficult and time-consuming to gather quantitative data.

Two approaches to the study of breeding behaviour demand such quantitative information. The first involves comparisons between species, with the objective of unravelling the adaptive significance of species-typical behaviour. The second is the experimental manipulation of variables believed to be affecting some aspect of the behaviour—a procedure needed, in many cases, to establish such effects. The fruitfulness of these two approaches has been demonstrated by the comparative and experimental studies on gull behaviour carried out in recent years by Tinbergen and his students (e.g. Tinbergen 1959, Tinbergen *et al.* 1962, Beer 1961-66, Cullen 1957, Kruuk 1964).

Since few ducks nest colonially, as the gulls do, the collection of information on the breeding behaviour of individual pairs is slow and laborious. But most ducks adapt well to confinement in pens and it is possible to gain insight into the behaviour of wild birds through the study of captives. Many species will breed in captivity even after being rendered flightless by clipping the primaries or by removal of the terminal digits of one wing ("pinioning"). But although much of

the behaviour of a pinioned duck seems to be unaffected by such an operation (e.g., the form of many courtship displays), social interactions involving aerial pursuit are impossible, and even energetic chasing of another bird on the surface of the water may be hampered. These difficulties are avoided by studying full-winged birds in large flight-pens.

This paper is the first in a series reporting such studies on the Shoveler *Anas clypeata*. This species is tame and breeds readily in captivity. Males exhibit pronounced territoriality during the pre-nesting and incubation periods but, despite their aggressiveness, birds do not kill one another when crowded. My main aims have been to document the characteristics of social interactions in breeding Shovelers under these conditions, and to investigate variables affecting the frequency and outcome of encounters. The information will provide a base for similar studies of other species and for experiments on effects of radiation on behaviour. This paper gives details of methods and procedure and correlates the frequency of certain behaviour patterns with the stages of the breeding cycle and time of day. Subsequent papers will deal in more detail with displays, pair-formation, and territorial behaviour.

The breeding conditions imposed on these Shovelers were artificial in four major respects. Firstly, the density of pairs was much higher than would be found in the wild. The pens covered 0.15 and 0.19 acre; the experiments, over five seasons, involved from four to seven pairs in a pen. The main effect of this crowding was to expose the pairs to almost constant sight of other Shovelers. Secondly, the movements of the birds were restricted; in particular, flights were greatly reduced in length and height. Thirdly, food was not evenly distributed in the pens. Although the ponds contained some live food, and the birds spent much time dabbling for it, a number of feeders were also included and these were used by more than one pair. Fourthly, the populations of pairs introduced to the study pens were stable throughout the breeding season; thus all birds quickly learned the identity of their pen-mates, and they were given no chance to react to strange individuals. In other respects, I believe the breeding conditions for these birds were not very different from those to be found in the wild.

The Flight-pens

In 1960, 1961 and 1962, observations were carried out in a rectangular pen measuring 127 feet × 51 feet × 16 feet high, located at the Delta Waterfowl Research Station in Manitoba (Figure 1). Three ponds, connected by ditches, were maintained at a constant level, several feet above the adjacent marsh, by an automatic pump. Clumps of grass for nesting sites (10 in 1960-61, 26 in 1962) were introduced. At the beginning of each breeding season the remaining ground was bare or sparsely covered, but a natural growth of grasses rapidly grew during the spring as a result of abundant irrigation from the ponds. When the vegetation grew very tall in June and July, some was removed by careful scything. A certain amount of natural food was available in the water, but pans supplied with grain were also placed in the pen (two in 1960-61, three in 1962). Small numbers of Blue-winged Teal *Anas discors*, Cinnamon Teal *A. cyanoptera* and Green-winged Teal *A. crecca carolinensis* were also kept in this pen. Observations were made from an elevated blind.

Experience with the Delta pen enabled me to design two improved flight-pens for more refined and intensive studies carried out in 1965 and 1966. The new pens are situated on a sandy field on the University of Minnesota's Cedar Creek Natural History Area, 30 miles north of Minneapolis. Each measures 90 feet × 90 feet × 12 feet high. They are adjacent, sharing a common wall, and both are overlooked by one elevated blind.

The Cedar Creek pens were designed to provide "ideal" breeding facilities for eight pairs (four in each pen) (Figure 1). Each contains a large pond, with the water level maintained at one foot by pumping from a well. Seepage is prevented by large sheets of plastic, protected underneath from burrowing rodents by a layer of chicken-wire. Pond edges are thin crusts of cement. The shape is square, with a square peninsula in the middle of each side. This configuration was intended to provide secluded corners in which birds would be out of sight of one another. A two foot wide strip of grass around the periphery of each pen provides the only nesting cover. The remaining land surface in the pens has quickly grown up in natural grasses but these areas are mowed several times each spring to eliminate other possibilities for nest-sites. A feed pan, which can be filled from outside the pen, and a floating

wooden frame to hold duck-weed (*Lemna*), are located in every corner. The plywood base of the wall separating the two pens was originally only two feet high, but this was extended to six feet in 1966, to prevent flying birds interacting through the wire.

The study birds

Most of the Shovelers used in the 1960-65 experiments were raised in captivity from eggs collected in the Delta area. A few birds were captured from the wild. In 1966, however, only birds raised in a natural way were used; most were captured from the wild in North Dakota as ducklings, a few were raised with their parents in the Cedar Creek pens.

The selection of strongly attached pairs proved to be a crucial step in the procedure. In order to secure the pairs needed in spring, a flock of 30 to 60 birds

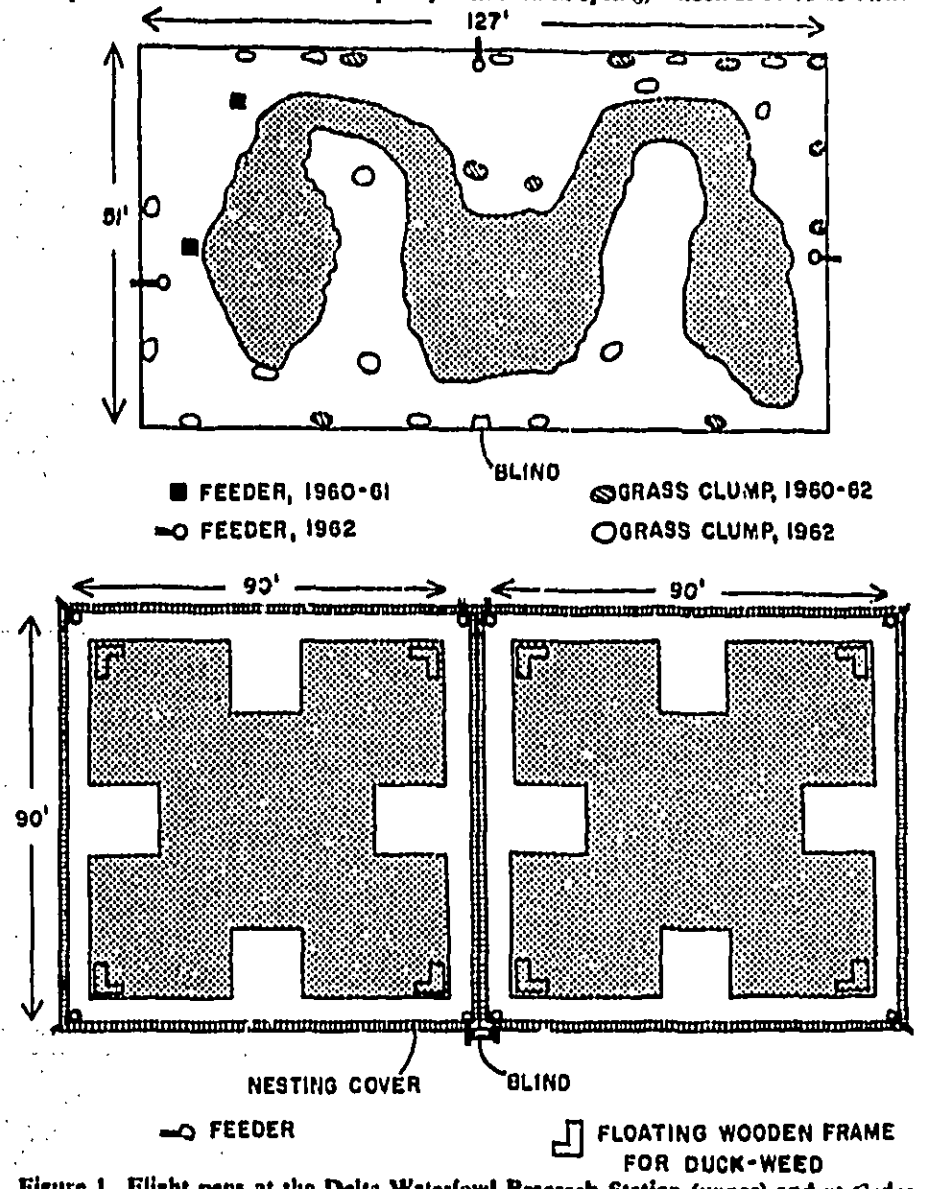


Figure 1. Flight pens at the Delta Waterfowl Research Station (upper) and at Cedar Creek Natural History Area (lower). See Photograph Section p. IX upper.

was maintained inside a heated building each winter. Pair-bonds were easily detected, especially by watching for the orientation of female Inciting movements, but many bonds were weak and care was taken to select only the strongest. Naturally, birds showing homosexual tendencies were not used.

In 1965 and 1966, the winter flock was divided into four visually isolated groups. Each of the four pairs used in a breeding pen was taken from a different group so that, as "pairs", they met for the first time in the breeding pen. Unfortunately, it was impossible to use individuals which had never seen one another before; the segregation covered only the period from November to May, during which the pair-bonds formed.

The birds were identified by combinations of colour bands and coloured nasal discs in the early years. Numbered nasal discs, similar to those described by Bartonek and Dane (1964), have proved invaluable in the Cedar Creek studies. (See Photograph Section p. IX lower.)

Procedure during breeding season

The birds were released into the breeding pens as early as possible in spring, usually during the first week of May. They were allowed to go through the breeding cycle with a minimum of interference until the ducklings were full grown. The inside of the pen was inspected briefly on about every third day. During the laying period, visits were delayed until late in the day when females had laid. Once incubation had started, birds were rarely flushed from their nests, and when small ducklings were present intrusions were avoided. As a result of these precautions I believe the behaviour of the birds was influenced very little by human intrusion, but my records on the fate of eggs and ducklings suffered correspondingly and are incomplete.

Observations at the Delta pen were not intensive and they were made on an irregular schedule. During the territorial phase in May and June my notes cover 15 hours in 1960, 8 hours in 1961, 21 hours in 1962. In 1965, at the Cedar Creek pens, observations were made for several hours on almost every day from 5th May to 30th June (total 175 hours). Whole-day watches from dawn to dusk (about 15 hours) were undertaken on five days. Fortunately the dates chosen were representative of the pre-laying and laying periods and the first, second and third weeks of incubation for most of the pairs. These records provided information on the relationship of activities to time of day, and they showed that the first few hours after sunrise are especially important if hostility, inspection of nesting cover, and egg-laying behaviour are to be studied. Since my main interest was in hostile behaviour, the observations in 1966 were made on the first three or four hours after sunrise (total 103 hours). The 1965 records also showed that daily observation is not essential if a representative sample of the interactions is to be obtained, and every third day was skipped in 1966.

Three experimental manipulations were carried out during the five years of study reported here. In 1962, the eggs were removed from two nests on the fifteenth and nineteenth days of incubation, so that behaviour during the "re-nest interval" could be studied. In 1965, all eight males were caught up on 5th June and held in crates for four hours and then released into the pens again. This treatment appeared to have little effect on the birds; they quickly returned to their territories and behaved in the same way as before their removal. In 1966, all males were removed from the pens for three hours on 24th May; they were transported to Minneapolis where two were irradiated. The results of this treatment will be reported elsewhere. As in the 1965 experiment, the birds quickly resettled when returned to their pens. In this paper, the two treated males are omitted from generalizations relating to behaviour of males after 24th May.

Breeding results

Only three of the 31 pairs used in these studies failed to lay eggs (Some pairs, or individuals, were used in more than one season; see Table I). Laying began 10-23 days after the birds were released in the breeding pens. Clutch-size varied between 4 and 11, with one instance of two females laying together to produce 13 eggs. The most frequent clutch-size was 8 (13 of 29 clutches). Incubation periods could not be determined precisely, since nests were not visited near the time of hatching. Estimates based on the first observations of ducklings suggest an average incubation period between 22 and 25 days. Two females remained sitting on dead eggs for at least 29 and 35 days. Hatching success was generally poor, only one female bringing off ducklings from all eggs laid, but there was much individual variation. Very few ducklings survived to reach maturity.

Sociability of pairs

During the first few days after introduction, pairs showed clear tendencies to be sociable, especially when choosing sleeping places. Thereafter, such tendencies disappeared almost completely until early June (Figure 2), when certain males began to associate while their mates were incubating. This behaviour was not highly developed, however, until the third week in June when hostility waned rapidly.

Establishment of territories

Hostility between pairs was observed from the day the birds were introduced to the flight pens. Threatening, chasing, and fighting activities increased during the first week and, in general, pairs were frequently involved in hostile encounters throughout May and the first three weeks of June (Figure 3).

Encounters between pairs included all possible combinations: threatening, chasing and fighting occurred between males, between females, and between members of the opposite sex. Most contacts involved chasing or threatening by a male directed at another male or at a female.

Localization of each pair's activities within the pen began to appear within a few days after introduction; rather clearly defined territories could be detected after a week or ten days. Every year, most pairs were successful in establishing a territory while one or two pairs were unable to do so effectively, at least during

Table 1. Breeding records for captive Shovelers.
* Eggs removed on 14th June. † Two females laying in same nest. (Ad) more than one year old; (y) yearling.

Year	Pairs Males	Pairs Females	Date pairs introduced to pen	Date first egg	Clutch size	Incubation period in days	Eggs hatched	Ducklings raised
1960	A (Ad)	A (Ad)	April 26	5.19	8	?	5	?
	B (Ad)	B (y)		5.22	8	22-23	6	
	C (y)	C (y)		5.26	8	24-25	0	0
	D (y)	D (y)		—	—	—	—	—
	E (y)							
1961	A (Ad)	A (Ad)	May 4	5.18	8	29+	0	0
	D (Ad)	D (Ad)		5.27	9	24-25	5	
	F (y)	F (y)		5.27	8	24-25	5	4
	E (Ad)	E (y)		6.9	5	22-23	4	
	G (y)							
1962	A (Ad)	A (Ad)	May 7	5.18	8	—*	—	—
				6.23	6	?	5	0
	D (Ad)	D (Ad)		5.21	13†	—*	—	—
	I (Ad)	I (?)		5.24	4	?	0	0
	G (Ad)	E (Ad)		5.31	8	24-25	?	0
	J (Ad)	J (y)		6.2	9	20-21	?	0
	E (Ad)	H (Ad)		6.7	4	?	?	0
	F (Ad)	F (Ad)		6.17	6	22-23	5	1
1965 Pen 1	15 (Ad)	13 (Ad)	May 5	5.15	8	35+	0	0
	2 (Ad)	4 (Ad)		5.16	7	24-25	5	
	14 (Ad)	8 (Ad)		5.18	9	24-25	2	4
	07 (Ad)	2 (Ad)		5.22	10	22-23	8	
1965 Pen 2	0 (Ad)	5 (Ad)	May 5	5.15	10	22-23	5	
	3 (Ad)	12 (Ad)		5.16	8	22-23	8	7
	12 (Ad)	10 (Ad)		5.16	10	22-23	3	
	5 (Ad)	7 (Ad)		5.18	8	25-26	4	
1966 Pen 1	0 (y)	0 (y)	May 3	5.17	8	24-25	7	
	1 (y)	1 (y)		5.24	8	23-24	7	5
	2 (y)	2 (y)		—	—	—	—	—
	3 (y)	3 (y)		—	—	—	—	—
1966 Pen 2	4 (y)	4 (y)	May 3	5.31	10	19-20	6	
	5 (y)	5 (y)		5.20	8	23-24	2	2
	6 (y)	6 (y)		5.23	11	22-23	5	
	7 (y)	7 (y)		5.24	11	22-23	6	

the early part of the breeding season. Most pairs continued to occupy the first area chosen throughout the season; a few switched to a new area.

Ritualized fighting was frequent between males, especially on the boundaries between territories or when two pairs were in dispute over one area. These fights characteristically involved vigorous circling on one spot, with much thrashing of wings on the water surface.

Inspection of nesting cover

Females were seen walking into nesting cover on the first or second day after introduction to the pens, as early as 27 days before laying began. Their males usually accompanied them closely, frequently disappearing into the grass also, and sometimes remaining there after the hen had walked out. Places were found where females had been turning round in the grass, but well developed scrapes, ex-

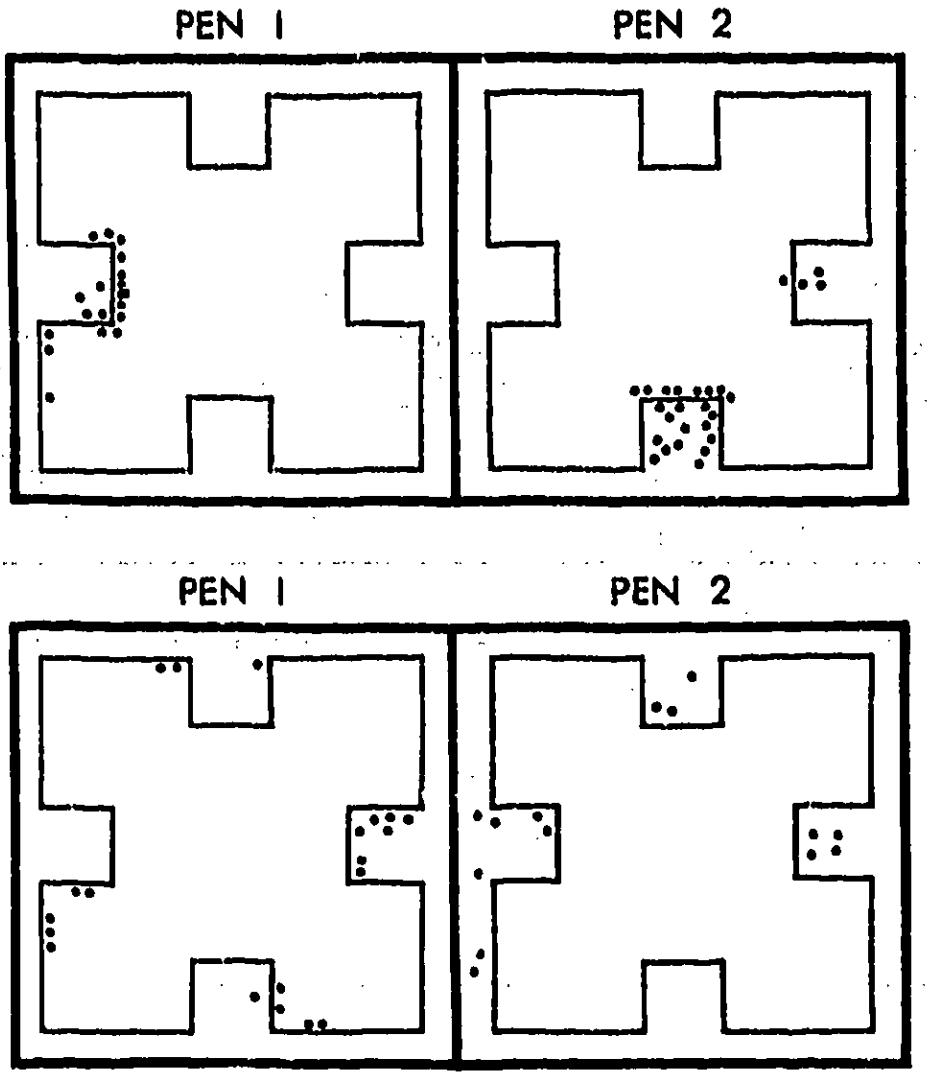


Figure 2. Decrease in sociability of captive Shoveler pairs illustrated by the distribution of sleeping sites on days 1 and 2 after introduction (upper) and days 13 and 14 (lower). Based on observations of 8 pairs, 4th, 5th May, 1966 (6 hours), and 16th, 17th May (8 hours).

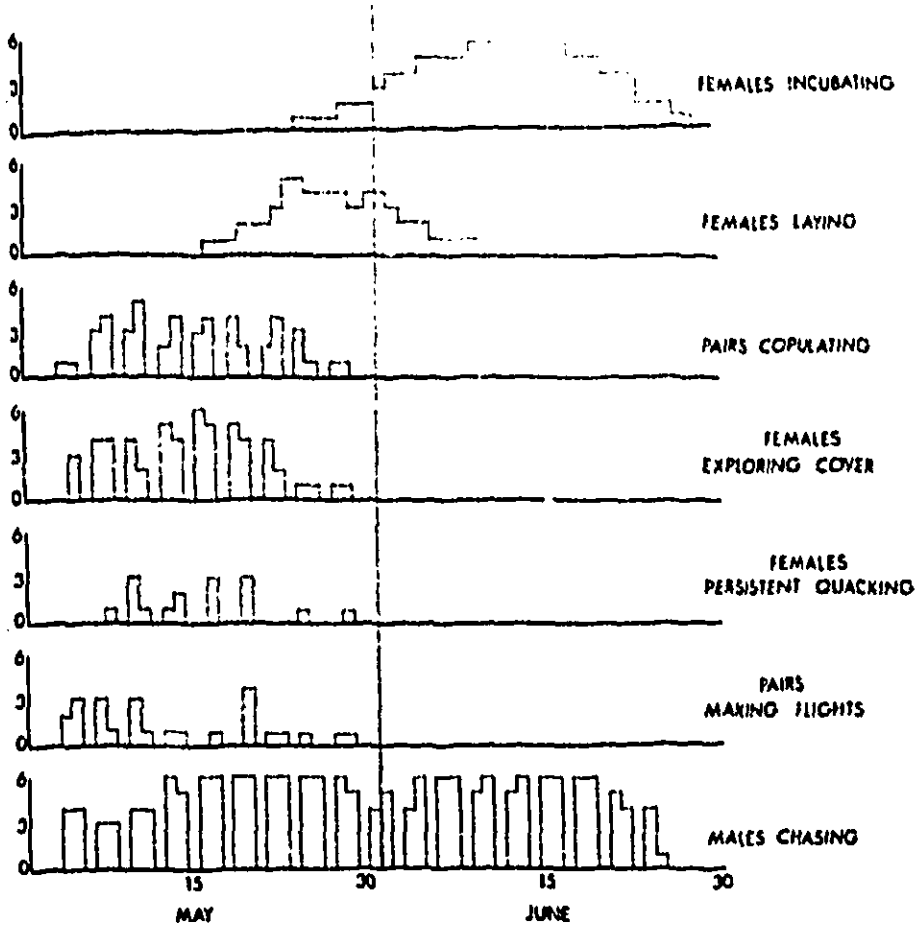


Figure 3. Number of captive Shovelers engaged in different activities during May and June, 1966 (maximum six pairs). Based on observation periods of 3 and 4 hours after dawn of every 3 mornings.

Table II. Frequency of records of percentage of time spent by six Shoveler females in cover or at the nest-site during four-hour observation periods beginning at sunrise (May-June, 1966).

	Percentages											
	<5	6-10	11-15	16-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100
13-27 days before laying	9											
5-12 days before laying	25	1	1									
1-4 days before laying	6	4	3			1		1				
First half of laying period	1			1	2	4	2	1	1	1	1	2
Second half of laying period							1	2	1	3	2	12

posing bare earth, were not found until around the fifth day. Thereafter, the number of scrapes increased steadily. By 16th May, 1966, the day before the first egg was laid, eight females had made a total of 18 scrapes.

The time spent by females in nesting cover increased during the one to four days preceding the laying of the first egg (Table II). In 1966, three females were recorded sitting on one or more scrapes for periods of 30, 31 and 129 minutes on the day before they laid their first eggs.

Most females were observed inspecting cover in the morning hours, especially during the first few hours after dawn (Figure 4). Many females ranged widely in different parts of their pen but chases often resulted when pairs intruded into territories. As a result, the location of scrapes and nests was influenced greatly by the areas where pairs could move without being chased. Some females showed a clear preference for one scrape several days before the first egg was laid, but others appeared undecided until the day of laying.

The details of the behaviour in cover could not usually be observed, but much time was spent walking slowly through the grass, squatting and turning round in depressions. Some scrapes were lined with grass before laying began while others showed bare ground exposed. On several occasions, females were seen to reach upward to pull grass down (the technique by which a canopy is formed) before eggs were laid. Inspection of cover, sideways-building, and pulling down movements were recorded in one or both of the two females which did not lay in 1966.

Within the week before laying and

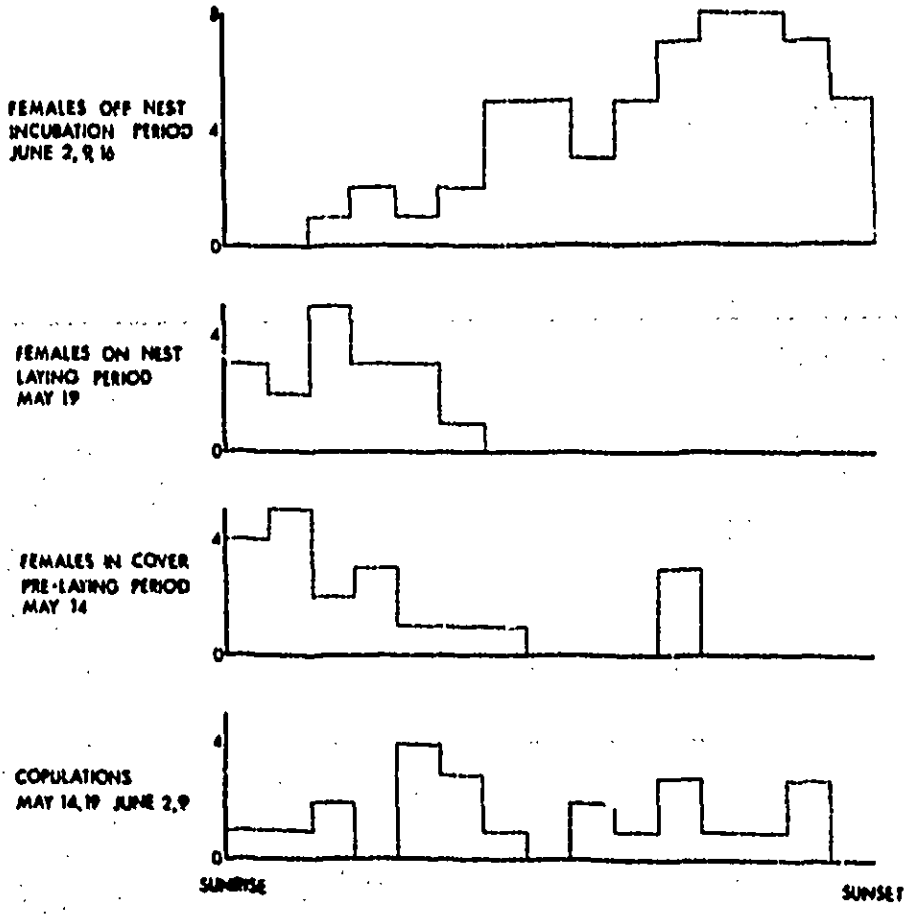


Figure 4. Nesting activities and copulations of captive Shoveler in relation to time of day during five dawn to dusk watches, 1965.

during the early days of laying females were observed making sideways building movements while sitting on open ground away from nesting cover or scrapes. On several occasions, these movements were seen just after a female had been at the nest to lay. Males were also observed making sideways building movements while sitting on open grass away from nest sites.

Copulations

Copulations were seen regularly from the day after introduction until the end of May. Most were seen during the pre-laying period, as early as 23 days before the first egg was laid, but some were also recorded during the laying period. The records for 1965 and 1966 show a drop in the frequency of copulations during laying. This might be expected since females were spending some time at the nest each day and so were "unavailable" for copulation, but the decrease is still apparent (for the first half of the laying period) when rates are computed on the basis of time when females were available (Table III).

was established that certain pairs may copulate twice in one day, others only once, others not at all. My records suggest that twice per day is usual during the period immediately before egg-laying begins. In four cases, during whole-day watches, pairs copulated at 09.49 and 15.42, 06.43 and 16.23, 09.24 and 17.53, 10.13 and 15.03, giving intervals of 5 h. 53 m., 9 h. 40 m., 8 h. 34 m. and 4 h. 50 m. In the course of morning watches, however, four instances of much shorter intervals were recorded: 06.35 and 09.35 (3 h.), 07.45 and 09.57 (2h. 12m), 04.57 and 07.25 (2 h. 28 m.), 04.58 and 07.32 (2 h. 34 m).

In most instances, mounting of the female by the male resulted in apparently successful copulation (120 records). Certain individual males, however, were unsuccessful in reaching the point of intromission, slipping off the female's back after mounting (10 records involving 6 males). In 15 instances, interruptions of pairs after the male had mounted resulted in incomplete copulation attempts. The close approach of another pair was usually effective in causing such an interruption

Table III. Frequency of copulations in relation to egg-laying by Shoveler (1965 and 1966).

	Days Before Laying					*Laying Period*	
	17-20	13-16	9-12	5-8	1-4	*First half*	*Second half*
Number of pairs observed	3	6	8	13	13	13	11
Pairs observed copulating	3	3	7	12	13	7	3
Successful copulations observed	6	3	9	26	28	8	3
Hours of observation when females off nest	32.5	73	93.3	163	228	186	35
Rate of copulations per female available per 24 hours of observation	1.48	0.16	0.29	0.29	0.23	0.08	0.19

Copulation was observed only three times during the incubation period and undoubtedly this is a rare event. This probably results from lack of adequate responses on the part of the females, since Pre-copulatory Pumping movements continue to be given at times by males, and a non-breeding pair continued to copulate up to 21st June in 1966.

There was no clear tendency for copulations to occur at certain times of day (Figure 4). During whole-day watches, it and typically copulations occurred when pairs were well apart from other birds.

Pair Flights and Persistent Quacking

Pairs frequently made flights around or across the pen during May. These were initiated in a characteristic way, being preceded by pre-flight movements, the birds standing in erect postures. With one exception, these flights ceased once egg-laying began (Table IV). Two non-breeding pairs continued to make flights up to 24th June, 1966.

Some females gave series of loud, harsh double quacks during the pre-laying period. This calling corresponds to the Persistent Quacking of the Mallard (= "Continuous Calls", Dzubin, 1957) but it appears to be less frequent in the Shoveler. It was recorded repeatedly in certain individuals but not at all in others. No clear correlation between calling and time of day was noted.

Rape attempts

The Shoveler is not one of the dabbling ducks which exhibits highly developed raping activity during the breeding season. Hostile interactions between pairs

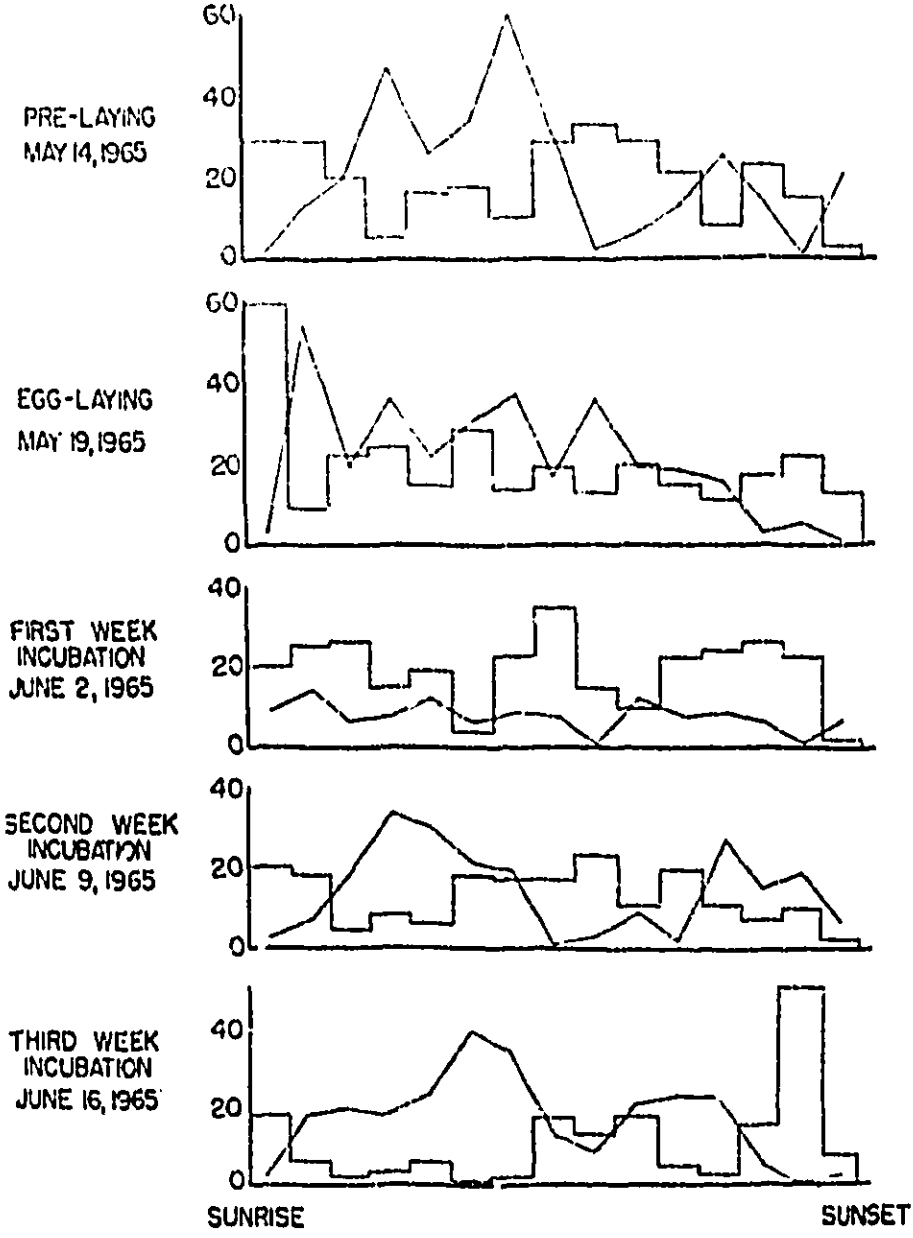


Figure 5. Number of male chases among Shovelers (histogram) and number of sleeping birds at 10-minute checks (line).

Table IV. Occurrence of flights around pen and Persistent Quacking in six Shoveler pairs, 1966.

Days before laying	*Total number flights*	*Number of pairs making flights*	*Number of females giving Persistent Quacking*	*Number of pairs or females under observation*
27	1	1	0	1
25-26	1	1	0	1
23-24	4	1	1	1
21-22	1	1	1	1
19-20	2	2	0	4
17-18	7	4	1	4
15-16	2	2	1	5
13-14	17	3	2	6
11-12	8	1	1	6
9-10	7	4	1	6
7-8	1	1	2	6
5-6	2	1	2	6
3-4	5	3	3	6
1-2	2	1	1	6
Days of egg-laying				
1-2	0	0	1	6
3-4	3	1	0	5
5-6	0	0	0	4
7-8	0	0	0	5
9-10	0	0	0	3
11-12	0	0	0	1

occurred daily throughout the territorial period and males frequently chased strange females, but clear attempts to rape were infrequent, and successful rape was rare. Only four instances of apparently successful rape were recorded during the five seasons. On 6th and 25th May, 1960, the female which did not lay was raped by the most aggressive male in the pen. On 6th May, 1965, and 13th May, 1966, rapes were observed involving females which had not begun to lay. The ability of most paired males to discourage the approach of other males by means of aggressive behaviour undoubtedly plays an important part in protecting females.

Egg-laying and incubation

Visits to the nest-site by females during the laying period were usually in the morning (Figure 4), but the precise times of laying are not known. Time spent on the nest each day increased during the laying period. During the first few days, most visits lasted one to two hours, but in the later stages of egg-laying many females were on their nests throughout the four-hour morning watches (Table II).

Although the nests were not visited every day it was established that females usually, but not always, laid one egg each day. In several instances, one or more days were missed, e.g. clutches of 7 or 8 eggs would not be complete until the tenth day. Furthermore, on 19th May, 1965, two females, which had already laid 2 and 4 eggs, did not visit their nests at all in the course of a dawn to dusk watch.

Incubating females left the nest at various times during the day, but most often in the late morning and afternoon (Figure 4). Sometimes females had two periods off, sometimes one, and in two instances females did not leave at all in the course of whole-day watches. The period off varied in length between about a half-hour and two hours. While off the nest, females bathed, preened, and fed with their mates.

Egg removal

Thirteen of 29 clutches were reduced by one or more eggs in the course of incubation and since nests were not visited daily a similar loss of eggs may have occurred in other nests without being detected. There was no evidence that egg predators were responsible, although rats were seen inside the Delta pen during one breeding season. The Cedar Creek pens appear to be effectively predator-proof. Three observations of females carrying an egg or egg shell from the nest suggest that this behaviour accounts for the disappearance of eggs from clutches.

The first observation was made on 8th

June, 1962. The female concerned had 2 eggs on 25th May, 3 on 28th May, 4 on 2nd June, and had 4 left in the nest after the removal was observed. Without more complete information it is impossible to explain the apparently slow laying schedule of this bird and to determine the stage of incubation at which the egg was removed. The eggs later dwindled to 3 and then 2; none hatched. The second observation was made by James March on 8th June, 1965. The female had been incubating a clutch of 10 eggs for two weeks; two days after the removal was witnessed she had 8 eggs. This clutch was subsequently reduced to 7 eggs, and 5 ducklings hatched. In both cases, the bird was seen to fly off the nest carrying an egg in the bill. Apparently the eggs had been pierced since they were carried in the tip of the bill and must have been grasped by a broken edge. After the birds alighted on water, the eggs were dropped and sank.

On 23rd June, 1965, James March saw a female fly off her nest carrying a broken egg shell in her bill, "freshly broken since yolk was still dripping from it." She dropped it in the water. On the next day this bird was found on the nest with newly-hatched ducklings under her.

On 22nd June, 1966, an empty egg shell, neatly cracked across the middle and half-opened, was found floating on the water. An egg was also seen floating on the surface on 27th June, 1965. These eggs must have been removed by females in the same way.

Throughout these studies, the presence of discoloured eggs was frequently noted when nests were checked during incubation. I suspect that some of these eggs are removed by females in the way described, but how they become broken is unknown.

Distraction Display

Incubating females were flushed from their nests occasionally and in many cases they flew on to the water nearby and made vigorous flapping movements with the open wings on the surface. Sometimes they gave loud quacks, at other times they merely opened the bill. These reactions were most frequent in the later stages of incubation.

Daily rhythms of sleeping and chasing activities

During the 1965 and 1966 observations, a record was kept every 10 minutes of the birds which were sleeping. A [illegible] sleeping activity occurred during the morning hours and there are indications of a secondary peak in the afternoon (Figure 5). Few birds were sleeping in the first hour after dawn or in the last hour or so before sunset. Usually the frequency of chasing activity is inversely correlated with the peaks in sleeping. This is especially clear in the case of the early morning burst of hostility. In several instances, however, both sleeping and chasing were infrequent during the last hour before sunset. This is probably correlated with a tendency for birds to feed actively just before sunset, but I cannot document this impression since daily variations in feeding behaviour were not recorded quantitatively.

The conspicuous peak in chasing activity in the late afternoon of 16th June (Figure 5) coincided with the time when a number of females were off their nests. Such an increase in male hostility often resulted when females joined their mates.

Broods

The behaviour of females with ducklings was not studied intensively. Probably this phase of breeding was more seriously affected by the pen conditions than any other. Ducklings ranged all over the pens, and were the cause of many hostile encounters. Females with broods often attacked ducklings from other broods, sometimes apparently killing them. This in turn lead to chasing and even fighting between females. Broods were also attacked when they passed close beside incubating females. Aggressive males attacked females with broods when they intruded in territories and in some instances the females fought back.

Although such conflicts no doubt accounted for some of the heavy duckling mortality, I suspect that shortage of food also played a part. In the last two years a determined attempt has been made to provide the young birds with an abundant supply of food in the form of duckweed (and the associated invertebrates collected with it) and prepared duckling pellets. But Shoveler ducklings spend a great deal of time dabbling in the water, and perhaps this effort has not been rewarded with a sufficiently rich return in the form of animal food.

Post-breeding moult

Males began to develop blotchy plumage in mid-June, and many were well advanced into the eclipse plumage by the

end of June. Most males were flightless between mid-July and mid-August, and had grown new primaries by the end of August. The single unpaired male was flightless much earlier than the paired males (by 5th July) in 1960. In 1961 the same individual male succeeded in displacing one of the paired males within a few days of introduction to the pen. This bird again moulted early (being flightless on 11th July), but the displaced male, who remained unpaired, did not lose his primaries early. Further studies are needed to determine whether unpaired males have a tendency to moult at a different time from paired males. Most females were not flightless until the middle or the end of August.

Discussion

The information on chronology of nesting-cover inspection, Persistent Quacking, pair flights, territorial hostility and copulation agrees well with what is known of these activities in wild Shovelers (e.g. Sowls 1955; personal observations). Variations in certain activities with time of day are also close to what might have been expected on the basis of field observations. The behaviour of females with broods, however, is likely to be highly unusual under such pen conditions, and much larger enclosures with fewer birds would be necessary to obtain natural behaviour.

These captive conditions appear to have influenced fertility and hatchability of eggs, and duckling mortality, in a number of ways. Shortage of ideal food and aggressive behaviour of females were probably involved in the poor survival of ducklings, but my information on the fate of eggs is too incomplete at this stage to yield more than suggestions on the factors involved in egg-loss.

The observations on egg removal, however, raise a number of interesting points. This behaviour is known to occur in wild ducks (e.g. Lindsey 1946, Hochbaum 1944) and Sowls (loc. cit.) has made experiments on egg shell removal by a wild Shoveler. The field observations suggest that females will remove broken eggs from a nest which has been only partly destroyed by a predator, and may return to continue incubation of the remaining eggs. Furthermore, many field workers have noted that eggs disappear from duck nests in the course of incubation for unknown reasons (e.g. Bezzel 1966). Sowls (loc. cit.) tentatively suggested that egg-removal by the hen might explain this phenomenon, and he also made the point that egg shell removal does *not* seem to occur at the time of hatching.

The observations on captive Shovelers support these suggestions. Two of the three cases where females were seen to fly off the nest carrying an egg in the tip of the bill involved nests being incubated. In the third case, hatching was in progress in the nest but the shell had yolk dripping from it, indicating that a duckling had not hatched from the egg concerned. The intriguing question is how the eggs become broken before removal.

I agree with Sowls that egg shell removal does not seem to be a regular occurrence in Shovelers at the time of hatching. Shells are often found in nests after the brood has left, and there are no observations indicating that shells from hatched eggs are removed at this time. Nevertheless, Sowls' experiments clearly demonstrated that females will remove shells during the incubation period. Presumably the situation is quite different from that revealed by Tinbergen *et al.* (1962) in the Black-headed Gull *Larus ridibundus*, where the removal of eggs at hatching is a regular event and has survival value in avoiding betrayal of the nest to aerial predators. The present meagre evidence suggests that incubating female Shovelers will remove addled or broken eggs during the incubation period, but will not remove shells at the time of hatching. An experimental approach to this problem would be rewarding.

Acknowledgements

My interest in the flight pen technique developed slowly in the course of observations on pinioned birds at the Wildfowl Trust and studies of wild birds at Delta. It is appropriate, as the Trust nears its twenty-first anniversary, that I first acknowledge my debt to Mr. Peter Scott for providing me with the opportunity to learn the advantages and limitations of captive waterfowl for behaviour studies. The Trust's magnificent collection has had a profound influence on many aspects of research, education, and conservation, but its leading role in fostering investigations of waterfowl behaviour has been especially obvious. I take great pleasure in paying tribute to Peter Scott for his tireless efforts on behalf of waterfowl and the study of their biology.

The studies at the Delta Waterfowl Research Station were supported by the Wildlife Management Institute. I am most grateful to Dr. Ira N. Gabrielson, Mr. C. R. Gutermuth, Dr. H. Albert Hochbaum,

Mr. Nan Mulder and Mr. Peter Ward for their encouragement and help. The Cedar Creek project was financed by the United States Atomic Energy Commission, Contract AT(11-1)-1332 (Publication C00-1332-33). I am indebted to Dr. John R. Tester, project leader, for assistance and advice of many kinds. For their important parts in facilitating the study I must thank Mr. Floyd H. Davis and the U.S. Fish and Wildlife Service banding crews in North Dakota and South Dakota for supplying birds, Mr. Forrest B. Lee and the Minnesota State Conservation Department for providing wintering quarters for ducks at the Carlos Avery Game Farm, Dr. William H. Marshall and Mr. Alvar Petersen for courtesies at the Cedar Creek Natural History Area, Mr. James R. March for assistance with observations, and Mr. Hugh House for invaluable practical help of all kinds. Mr. David Strohmeyer gave helpful comments on the manuscript.

References

BARTONEK, J. C. and G. W. DASE. 1964. Numbered nasal discs for waterfowl. *J. Wildl. Mgmt.* 28(4) : 688-692.

BEER, C. G. 1961-1962. Incubation and nest building behaviour of Black-headed Gulls. *Behaviour* 18(1-2) : 62-106; 19(4) : 283-304; 21(1-2) : 17-77; 21(3-4) : 11-176; 26(3-4) : 189-214.

BLZZEL, E. 1966. Zur Ermittlung von Gelegegrösse und Schlüpferfolg bei Entenvögeln. *Die Vogelwelt* 87(4) : 97-106.

CULLEN, E. 1957. Adaptations in the Kittiwake to cliff-nesting. *Ibis* 99 : 275-302.

DZUBIN, A. 1957. Pairing display and spring and summer flights of the mallard. *Blue Jay* 15 : 10-13.

HOCHBAUM, H. A. 1944. *The Canvasback on a prairie marsh.* Amer. Wildl. Inst., Washington, D.C.

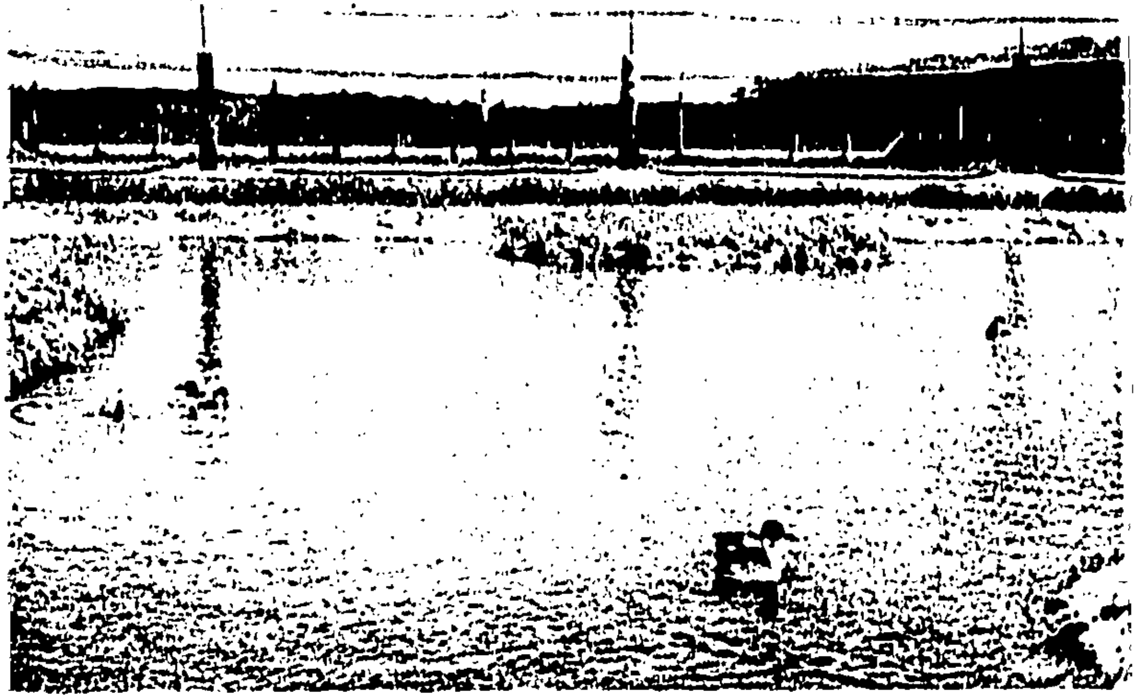
KRUUK, H. 1964. Predators and anti-predator behaviour of the Black-headed Gull (*Larus ridibundus* L.). *Behaviour Supplement XI.*

LESSLEY, A. A. 1946. The nesting of the New Mexican duck. *Auk* 63 : 483-492.

SOWLS, L. K. 1955. *Prairie Ducks.* Wildlife Management Institute, Washington, D.C.

TINBERGEN, N. 1959. Comparative studies of the behaviour of Gulls (Laridae): A progress report. *Behaviour* 15(1-2) : 1-70.

TINBERGEN, N., G. J. BROEKHUYSEN, F. FEEKES, J. C. W. HOUGHTON, H. KRUUK and E. SZULC. 1962. Egg shell removal by the Black-headed Gull (*Larus ridibundus* L.): a behaviour component of camouflage. *Behaviour* 19(1-2) : 74-117.



Upper: Shoveler pairs [illegible] well defined territory [illegible] one of the [illegible] pools at Cedar Creek Natural History Area, Minnesota. See page [illegible]

— McKINNEY

Lower: A pair of the Shoveler [illegible] with [illegible] plastic [illegible] — McKINNEY